THE CHANGES IN RESPIRATION AT THE TRANSITION FROM WORK TO REST. BY A. KROGH AND J. LINDHARD.

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WE have in previous papers called attention to the changes in the physiological state of the body especially regarding the respiratory functions at the transition from rest to work and during the initial stages of muscular work either voluntary or electrically induced (1, 2). In the present paper we propose to deal with another transitional state, namely the transition from work to rest.

We have made use of Krogh's bicycle ergometer and respiration apparatus described in detail elsewhere (3). After a working period of variable length and intensity the work was stopped suddenly, and the subject placed his feet on the foot-clamps of the ergometer. Thus the experiments after work were made in the same position of the subject as were the resting experiments made before work began and they may be compared directly with the latter.

Usually the first respiration experiment began about ·2 minute after cessation of work and lasted about half a minute, the later experiments lasted a minute or a little more. In addition to the respiration experiments *b*-samples of alveolar air were drawn corresponding more or less closely to the former. As however the values for the metabolism calculated from the *b*-samples and the calculated alveolar ventilation differ some 10 per cent. from the results of the respiration experiments, and as the correction to be introduced is not constant owing to the fact that the *b*-samples to a certain degree depend on the mechanics of respiration, we do not think it of sufficient interest to deal with the alveolar samples, especially, as the results obtained from these on the whole only differ from the results of the respiration experiments in showing a somewhat greater variability.

In the following pages the main results will be dealt with; some protocols are given at the end of this paper to illustrate the details of the experiments.

Ventilation. A glance at Fig. 1 and Figs. 1 and 2 in the previous paper (1) dealing with voluntary muscular work will suffice to show that the changes in ventilation taking place, when passing from work to rest, have quite another character than those found when passing from rest to work. In the latter case the ventilation curve presents a sudden very marked rise while the curve, when work has ceased, only gradually and rather slowly falls to the resting level. The very moment, when work ceases, cannot as a rule be recognised on the curve. Running parallel with the decrease in ventilation we find a more uniform decrease in frequency and depth of respiration. After severe work the functions named may nearly reach the resting level within some 10 to 15 minutes.

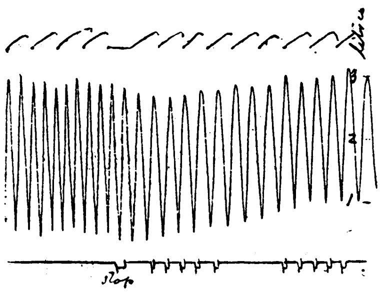
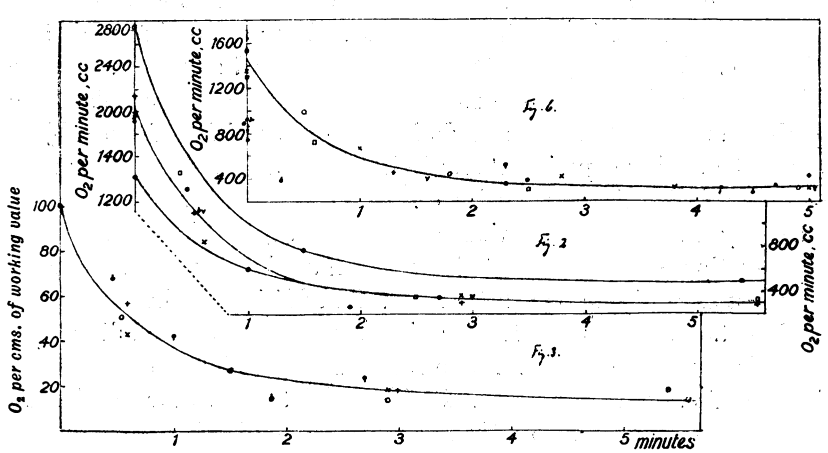


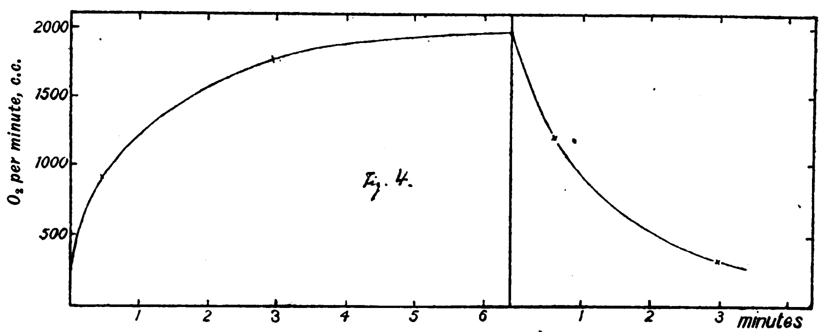
Fig. 1. Time marker ·1 minute.



Respiratory exchange. The oxygen intake decreases rapidly, when work is stopped, and reaches in about three minutes a fairly constant level, the height of which depends on the intensity of the preceding work. During the following minutes the fall in the curve is as a rule very slow, and if the work performed has been vigorous the respiratory exchange, as pointed out by Durig and Zuntz (4), does not return to the resting level for at least five hours or even for two days or more (5). Fig. 2 shows the decrease in the oxygen consumption in the first five minutes after work has ceased. The curve corresponding to Exp. I lies somewhat higher than the rest, and the curve for Exp. II at least at the beginning a little lower owing to the higher resp. lower starting point in these experiments. If, however, we start from the last working value and calculate the percentage decrease, all experiments may fairly well be represented by a single curve, indicating that the decrease takes place in a very uniform manner (Fig. 3).

We have pointed out (1) that at the transition from rest to work the oxygen intake does not rise instantaneously though certainly very rapidly to a level corresponding to the amount of work performed. The time elapsing before the level has been reached cannot be determined with certainty from our experiments because the work was not kept constant. Liljestrand and Stenström (6), however, have shown that even a level corresponding to 3000 c.c. O_2 per minute with fairly constant work may be reached in about ·8 minute. In other cases, perhaps owing to a less abrupt beginning of work, it will last somewhat longer, in some experiments of ours 2–3 minutes. As the mechanical efficiency of the subject cannot be determined independently of the respiratory metabolism, we had no means of deciding whether the oxygen deficit, arising, say, in the first minute of work, is regained during the working period or not. The experiments dealt with here show clearly, that the loss is not, or at all events not to any appreciable extent, recovered during work. In Exp. VIII we have determined the curve for the oxygen absorption in the first minutes of work as well as the curve for the same function after work has ceased. A measurement (planimetric) of the two areas bordered by the O-ordinate, a line representing the level of the oxygen curve and this curve itself, resp. the ordinate corresponding to stoppage of work, the oxygen curve after work and the resting level, will prove, that these areas are approximately equal in size (Fig. 4). In the present case each area represents about 1850 c.c. of oxygen. The total amount of oxygen available in the blood at the beginning of work is about 750 c.c., and of this not more than two-thirds can possibly be taken up by the working muscles. The oxygen deficit of the muscles during work is therefore at least 1350 c.c. This deficit must represent the anoxybiotic reactions which take place during the first phase of the contraction process and which are not finally made up by oxidation until after the work has ceased.

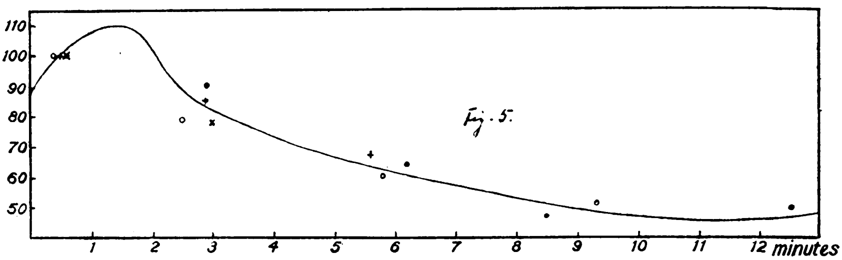
Regarding the fact that the oxygen consumption at the beginning does not correspond to the work performed, we thought it might be possible, when very severe work was started suddenly and then stopped again before the corresponding level of the oxygen curve had been reached, to get a rise in the oxygen intake after the cessation of work. We made two experiments to try this possibility but were disappointed in our expectations. In the first case (IV) the work was obviously too small in amount and had lasted too long. In the second (VII), lasting ·52 minute, the work was very vigorous, corresponding to 2310 kgm. per minute. The oxygen absorption was not determined, but in another experiment, in which the work was but insignificantly higher, we found an oxygen consumption of 2820 c.c. per minute ·52 minute after the beginning of work. In the present case, a respiration experiment ·40 minute after work gave 1455 c.c. O_2 per minute, and an alveolar sample ·15 minute after work gave 1565 c.c. per minute. Even if the last named determination is somewhat unreliable, there can be no doubt about the result, that the oxygen consumption has decreased rapidly as soon as



work was stopped. On the other hand it is extremely probable, that the total "oxygen area" has been greater after than during work.

The respiratory quotient in two experiments (II and III), representing the least heavy work, was falling at the transition from work to rest, to regain in a couple of seconds the working value. In four experiments with heavier work the quotient rose, when work was stopped, and rose above unity. In two experiments (IV and VII), finally, the working quotient was not determined, but after work the quotient was in both cases very high and must be considered to belong to the second group. If in the Exps. V–VIII we take the value from the first experiment after work as starting point and calculate the proportionate decrease, the values from these four experiments may be represented by a single curve (Fig. 5). The most characteristic feature met with seems to be a marked rise, the more pronounced as the work becomes more and more heavy, followed by a fall to subnormal values, *i.e.* values below ·7. Yet the values found in the first respiration experiment after work do not represent the highest figures for the quotient. Alveolar samples drawn just before and after this experiment show, that the quotient rises somewhat higher, the turning point of the curve may be supposed to lie one minute and a half after work has ceased and amount to some 110 per cent. of the figure from the respiration experiment. How these regular variations are to be explained is at present not quite clear, but a likely explanation may be, that the lactic acid produced in the muscles during work perhaps in connection with a persistent increase in the excitability of the respiratory centre leads to a washing out of CO_2 and thus raises the quotient. When the lactic acid has been eliminated and the centre has regained its normal excitability the accumulation of CO_2 causes the quotient to decrease.

If we consider *the alveolar CO_2 tension* in Exps. V–VIII, it results



that in the first period (*i.e.* half a minute to three minutes after work has ceased) the alveolar tension is constant or somewhat decreasing (cp. Protocols VI–VIII). The *b*-samples mentioned seem to show that this movement is real; there are no signs indicating a wave corresponding to the rise and fall in the quotient in the same interval. From about the third minute the alveolar CO_2 tension rises slowly, symmetrical with the simultaneous fall in the quotient. In Exps. I–III there was likewise a fall in the alveolar tension in the first minute after work, but the transition from work to rest acted in a different manner in the two groups of experiments. In Exps. I and II the alveolar CO_2 tension rose, when work was stopped, in Exp. III it did not alter and in the following experiments we find a more or less marked decrease. These changes do not appear to have any relation to the working level of the alveolar tension.

The behaviour of the quotient within the first three minutes in connection with the simultaneous washing out of CO_2 may indicate the appearance of fixed acids in the blood. The subsequent rise in the tension may thus be due to the successive elimination of these acids.

Regarding *the electrically induced work* in the Bergonié chair we may refer to our previous paper (2). The experiments dealt with here have been made in continuation of the work-experiments already described. The considerable variation in the results from such experiments compared with those from experiments on the ergometer, is evident also in the experiments after work. There can be no doubt, however, that the essential features met with are similar, whether the work has been voluntary or electrically induced.

Concerning the mechanics of respiration, the ventilation in the work-experiments is disproportionately high compared with the oxygen consumption, and the decrease, when work is stopped, is very marked. The frequency of respiration behaves in quite a similar manner, while the decrease in depth proceeds after nearly the same scale as that found after voluntary work.

The decrease in the oxygen metabolism is shown in Fig. 6. A comparison between this figure and Fig. 2 will prove, that the first-named presents a less marked fall and, at least within the first three minutes, maintains a somewhat higher level than the latter. The different shape of the curves may partly be due to the fact, that the working level is as a rule remarkably higher in voluntary than in electrically induced work, but it cannot be doubted, that the return to the resting level in the Bergonié experiments shows a more protracted course than in the ergometer experiments. Besides certain irregularities are usual; a lower value preceding a higher is not uncommonly met with. In one experiment we have quite an inverse curve for the oxygen absorption. The first value—1·25 minutes after cessation of work—is remarkably low, far below the value found at rest, and since the respiration during the experiment is interrupted by long pauses, more or less unreliable. Then the oxygen absorption rises and at 9 minutes after work it amounts to 445 c.c. per minute, *i.e.* 100 c.c. above the resting level on this day.

The respiratory quotient is in the Bergonié experiments first and foremost depending on the respiration during the preceding work. In most cases the quotient during work is disproportionally high and then exhibits a sudden decrease at the transition from work to rest. The decrease is often continued in the following minutes, and the quotient may reach astonishingly low values. In one subject (R.E.) the quotient varies in a different manner. Though the working value in the first experiment is 1·40, the quotient rises after work to 1·50 and then in a few minutes it decreases to the subnormal value ·385. In the second experiment the working level of the quotient was exceptionally low, only ·635, and was after work raised to ·86.

In accordance with the high respiratory quotient during work the alveolar CO_2 tension was often extremely low, in some experiments below 20 mm. Hg.; when work ceases, it rises suddenly to about the resting value.

SUMMARY.

The changes in respiration brought about by muscular work only gradually return to the resting level, when work is stopped.

The oxygen deficit caused by the lagging behind of the oxygen absorption in the first minute or minutes of work is not compensated during work but may be determined quantitatively, when work has ceased.

When heavy work has ceased, the respiratory quotient rises, often far above unity, and the increase is continued during about one minute and a half. The quotient then decreases in some cases to subnormal values. The initial rise may be due to washing out of CO_2 caused by fixed acids in the blood.

The changes in respiration taking place after electrically induced work are on the whole similar but much more irregular than those following voluntary work.

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PROTOCOLS OF REPRESENTATIVE EXPERIMENTS.

I. *Voluntary work.*

Time after cessation of work min.	Duration of exper. min.	Respirations	Frequency per m.	Ventilat. direct, L.	Depth of respir.	Ventilat. per m. at 0°760 mm. dry	Metabolism per minute, c.c. CO_2	Metabolism per minute, c.c. O_2	R.Q.	Alveolar CO_2 tension %	Kgm. per min.
1	2	3	4	5	6	7	8	9	10	11	12
VI. 24. xi. 15. J. L. Ergometer. Duration of work, about 20 min. Load 2·0 kg.											
Rest	1·14	8	7·0	6·34	793	5·09	177	210	·84	4·48	
After work											
− 2	1·05	27	25·5	57·2	2220	49·6	1890	1960	·965	4·22	840
+ ·6	·61	12	19·7	21·5	1790	32·1	1050	837	1·30	3·85	
+ 2·9	1·095	16	14·6	21·0	1310	17·45	421	360	1·17	2·89	
+ 6·2	1·00	9	9·0	9·38	1040	8·54	238	287	·83	3·35	
+ 8·5	1·13	10	8·85	8·50	853	6·87	209	341	·615	3·77	
+12·5	1·12	8	7·1	7·30	914	5·94	196	307	·64	4·05	
VII. 1. xii. 15. J. L. Ergometer. Duration of work, ·52 min. Load, 3·0 kg.											
Rest	1·49	12	8·05	9·70	807	5·98	205	226	·88	4·41	
After work											2310
+ ·40	·454	14	30·6	36·7	2620	74·5	•2530	1455	1·74	3·80	
+ 2·5	·96	14	14·6	16·3	1164	15·65	482	350	1·38	3·78	
+ 5·8	1·25	12	9·6	13·2	1100	9·72	332	317	1·045	4·09	
+ 9·3	1·31	12	9·2	11·3	941	7·95	279	314	·89	4·32	
VIII. 8. xii. 15. J. L. Ergometer. Duration of work, 16 min. Load 2·0 kg.											
Work											
+ ·45*	·539	10	18·5	15·6	1558	25·95	997	912	1·09	4·45	784
+ 2·9	1·13	22	19·5	57·1	2595	45·0	1940	1765	1·10	4·85	
+ 6·4	1·10	24	21·8	55·6	2320	45·0	1895	1955	·97	4·78	
+ 9·4	1·15	24	20·8	55·7	2320	43·0	1815	1820	·995	4·78	
+14·4	1·15	24	20·8	55·8	2325	43·2	1830	1970	·93	4·90	
After work											
+ ·6	·57	9	15·8	18·6	2070	29·1	1135	1105	1·03	4·69	
+ 3·0	1·24	11	8·9	10·6	962	7·60	275	322	·805	4·70	

* In the work experiments the figures indicate time from beginning of work.

PROTOCOLS OF REPRESENTATIVE EXPERIMENTS.

II. *Induced work.*

Time after cessation of work	Vent. per minute L.	Frequency of respiration	Depth of respiration c.c.	Metabolism per minute, c.c. CO_2	Metabolism per minute, c.c. O_2	Respiratory quotient	Alveolar CO_2 tension %	Pulse-rate
1	2	3	4	5	6	7	8	9
IV. 18. v. 15. A. K. Bergonié. Duration of work, 19·5 min.								
Rest	—	—	—	—	264	·935	4·78	70
Work								
−1·5	61·9	55·4	1118	1075	933	1·15	2·51	96
+2·3	8·20	17·5	468	209	360	·58	4·87	
+4·7	8·41	18·3	460	213	336	·635	4·83	75
V. 1. v. 15. H.P.L. Bergonié. Duration of work, 14 min.								
Rest	—	—	—	—	262	·80	5·24	
Work								
−1·4	42·2	20·5	2060	1500	1540	·975	4·57	
+ ·5	26·45	21·6	1225	965	990	·975	4·93	96
+1·8	13·8	16·9	815	471	438	1·075	5·00	72
+4·9	10·1	16·7	605	296	318	·935	4·81	
VIII. 14. v. 15. J. L. Bergonié. Duration of work, 23 min.								
− ·5	61·1	23·95	2552	1490	1310	1·12	3·15	118
+ ·6	23·5	14·5	1613	692	720	·96		
+2·5	6·20	7·05	879	195	303	·645		
+5·7	6·28	7·45	841	203	329	·62		
X. 26. v. 15. J. L. Bergonié. Duration of work, 26 min.								
− ·5	51·8	22·0	2350	1420	1365	1·04	3·35	110
+1·0	12·9	9·7	1330	478	664	·72	4·70	
+2·8	9·03	7·95	1137	306	408	·75	4·48	
+5·0	7·88	8·2	960	266	322	·825	4·59	